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Research

Below- and aboveground traits explain local abundance, and regional, continental and global occurrence frequencies of grassland plants

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Plants vary widely in how common or rare they are, but whether commonness of species is associated with functional traits is still debated. This might partly be because commonness can be measured at different spatial scales, and because most studies focus solely on aboveground functional traits.

We measured five root traits and seed mass on 241 central European grassland species, and extracted their specific leaf area, height, mycorrhizal status and bud-bank size from databases. Then we tested if trait values are associated with commonness at seven spatial scales, ranging from abundance in 16-m^2 grassland plots, via regional and European-wide occurrence frequencies, to worldwide naturalization success.

At every spatial scale, commonness was associated with at least three traits. The traits explained the greatest proportions of variance for abundance in grassland plots (42%) and naturalization success (41%) and the least for occurrence frequencies in Europe and the Mediterranean (2%). Low root tissue density characterized common species at every scale, whereas other traits showed directional changes depending on the scale. We also found that many of the effects had significant non-linear effects, in most cases with the highest commonness-metric value at intermediate trait values. Across scales, belowground traits explained overall more variance in species commonness (19.4%) than aboveground traits (12.6%).

The changes we found in the relationships between traits and commonness, when going from one spatial scale to another, could at least partly explain the maintenance of trait variation in nature. Most importantly, our study shows that within grasslands, belowground traits are at least as important as aboveground traits for species commonness. Therefore, belowground traits should be more frequently considered in studies on plant functional ecology.

Keywords: commonness, functional traits, naturalization, plant economics spectrum, rarity, root tissue density, root traits, species distribution

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Introduction

Flowering plants are estimated to have diversified into an extant global flora of about 369 000 species (Willis 2017). Most of those species have small ranges and maintain low population densities, and are thus considered rare (Enquist et al. 2019). On the other side, a few species are considered common or dominant, as they achieve high population densities and have colonized large stretches of land and many regions around the world (Ulrich et al. 2010, Pyšek et al. 2017). Although this pattern has been recognized as early as the 19th century (Darwin 1859), the reasons why most species are rare and a few are common or dominant are still unclear (Gaston 2011).

Plant functional traits have been successfully used to explain species occurrence patterns in relation to environmental conditions (Violle et al. 2007). It has also been shown that species with particular trait values increase in abundance when filtered by the environment (Lavorel and Garnier 2002). About two decades ago, Murray et al. (2002) reviewed studies that compared traits between common and rare species. They found 54 such studies, but most of those included very few species, which made it difficult to draw any general conclusions. Since then more and larger studies have compared traits of common and rare species (Cadotte and Lovett-Doust 2002, Cornwell and Ackerly 2010, Gabrielová et al. 2013, Arellano et al. 2015). Nevertheless, drawing general conclusions is still difficult as the studies vary in the traits included and in how common and rare plants were defined. The latter is not surprising as commonness (or rarity) has multiple dimensions (Rabinowitz 1981) and can apply to different spatial scales. For example, while a species may be locally abundant in a certain habitat type (i.e. be common), it might have a restricted distribution globally (i.e. be rare). As a consequence, the importance of traits for commonness may depend on the spatial scale considered. For example, it is conceivable that large-seeded species have a competitive advantage resulting in high local abundances, whereas small-seeded species might disperse more widely resulting in higher occurrence frequencies at larger spatial scales (Westoby et al. 1992).

The vast majority of studies relating traits to ecological parameters are focussing on aboveground traits, and consequently such traits are overrepresented in trait databases (Laliberté 2017). Although leaf traits, plant height and seed weight are considered to capture most variation in plant form and function (Westoby 1998, Díaz et al. 2016), it has been shown that inclusion of belowground traits can substantially increase predictive power for species distributions (Klimešová et al. 2016). Indeed, as roots are important for anchorage, storage and the uptake of water and nutrients, belowground functional traits might actually be crucial drivers of a species' abundance and occurrence frequency. Nevertheless, to the best of our knowledge, so far none of the studies comparing rare and common species has included belowground functional traits (Cadotte and Lovett-Doust 2002, Cornwell and Ackerly 2010, Gabrielová et al. 2013, Arellano et al. 2015). One reason why belowground traits are only rarely considered in plant functional trait analysis is that their measurement is technically challenging and labour intensive (Freschet and Roumet 2017). Another reason is that it is frequently assumed that belowground traits are correlated with aboveground trait (Pérez-Ramos et al. 2012, Reich 2014, Shen et al. 2019). For example, leaf manganese has been shown to correlate with root traits related to phosphorus acquisition strategy (Lambers et al. 2015), and shoot blumenols with the interaction of roots with arbuscular-mycorrhizal fungi (Wang et al. 2018). However, several recent studies show that correlations between above and belowground traits vary tremendously among clades (Valverde-Barrantes et al. 2017) and depend on the traits considered (Kembel and Cahill 2011, Kramer-Walter et al. 2016, Weemstra et al. 2016, Bergmann et al. 2017, Ma et al. 2018) as some evolutionary drivers are unique to roots (Bergmann et al. 2020).

We tested if plant functional traits explain the commonness of species across spatial scales from local abundance in grassland plots to their worldwide distribution. To do so, we measured root traits and seed weight on 241 grassland species grown in two large common-environment experiments. In addition, we extracted aboveground traits, bud-bank traits and mycorrhizal status from databases. We then tested how the traits relate to the abundance and occurrence in grassland plots of the German Biodiversity Exploratories (Fischer et al. 2010), the occurrence frequency across Germany, the occurrence frequency across the European and Mediterranean native region, and their global occurrence as naturalized alien species. We aimed to answer the following questions: 1) Do plant functional traits explain species commonness, i.e. abundance and occurrence frequency across spatial scales? 2) Do the contributions of traits to species commonness vary with the spatial scale considered? 3) Do above- and belowground traits contribute differently to explaining species commonness?

Material and methods

Species traits

Species selection, seed material and precultivation

The species used are herbaceous angiosperms occurring in the grassland plots of the German 'Biodiversity Exploratories' (Fischer et al. 2010, Socher et al. 2012). In each of three regions of Germany, the Schwäbische-Alb (south-western Germany), Hainich-Dün (central Germany) and Schorfheide-Chorin (north-eastern Germany), 50 plots (4 × 4 m) were selected in grassland habitats covering a wide range of land-use intensities. From 2008 to 2016, the vegetation composition of each of the 150 plots was assessed annually in late spring by estimating the cover of each species. We standardized the species names according to the accepted names in <www.theplantlist.org>, accessed 15 June 2019, using the *Taxonstand* package (Cayuela et al. 2012) to allow us to align the species names between different distribution and trait datasets. In total,

363 vascular plant species have been identified in the plots of the 'Biodiversity Exploratories'. For 311 of those species, we were able to obtain seeds from commercial seed suppliers or botanical gardens for our experiments (Supplementary information). For *Alchemilla vulgaris agg.*, which also includes taxa that are difficult to distinguish from *A. vulgaris*, we used seeds from *A. vulgaris*. For *Leucanthemum vulgare agg.*, which includes both *L. vulgare* and *L. ircutianum*, we used seeds from both species and the trait values were averaged.

In two experiments, we measured functional traits on those species. Before the first experiment, we individually weighed 10 seeds, randomly chosen from the supplier's bag, for each of the 311 species. Then we did an indoor pot experiment to determine root morphology of the species, and an outdoor pot experiment to determine rooting depth. For both experiments, seeds were first sown in plastic pots (7 × 7 × 6.5 cm) filled with peat soil. The pots were then placed in a growth chamber for two to three weeks (night/day 9/15 h; 18/21 ± 1.5°C; relative humidity 90 ± 5%) before transplanting the seedlings into the pots used for the experiments (for cultivation times, see Supplementary information). In addition to the traits measured in the experiments, we obtained data on aboveground traits (specific leaf area, height), bud-bank size and mycorrhizal status from databases.

Experiment on root-system morphology

From 1 May to 6 October 2017, we performed a glasshouse experiment to measure root-system morphological traits of the study species. As root morphology might depend on nutrient availability, we grew half of the plants per species at intermediate nutrient levels and the other half at high nutrient levels, after which we averaged the trait values per species. Because of the large number of species and the time-consuming measurements, we grew the plants in four temporally shifted (4–6 weeks) batches. We aimed to have each species represented in each batch, and to have a total of seven replicates per species and nutrient level across all batches (Supplementary information). The seedlings of the species that had germinated (n = 233) were transplanted individually into plastic pots (1.3 l) filled with a mixture of sand and vermiculite (1:1 volume ratio). The pots were then randomly allocated to positions in two glasshouse compartments, and allowed to grow for four weeks (night/day 10/14 h; 22/28 ± 1.5°C; relative humidity 80 ± 15%). Plants were fertilized three times a week with either an intermediate nutrient solution (40 ml with 1500 µM KNO_3) or a high nutrient solution (40 ml with 12 000 µM KNO_3). The fertilizer was a modified version of the Hoagland recipe (Supplementary information).

We grew the plants for four weeks only to avoid roots becoming pot-bound, to be able to analyse the entire root systems and to ensure that all the belowground biomass was formed by roots, excluding rhizomes. After washing off the substrate, the root system was cut below the collar and stored for <1 week in a plastic tube filled with distilled water at 4°C. Then, root systems were spread individually in a thin layer of water in transparent trays (11 × 11 cm) and scanned at 800 dpi with a flatbed scanner modified for root scanning (Epson Expression 10 000 XL and 11 000 XL). The images were analysed using the software WinRHIZO 2017a to obtain the total root length and root volume. Root systems were then oven-dried for >48 h at 65°C and weighed. We calculated specific root length by dividing the total root length by the belowground dry biomass, and root tissue density by dividing the belowground dry biomass by the sum of the root volumes according to Rose (2017). The diameter of fine roots (i.e. distal roots), thought to be the most important roots for nutrient uptake (Freschet and Roumet 2017), was determined by randomly sampling a distal root branch (or a portion of it) for each root system and calculating the mean of the external–internal links diameter obtained with the 'Link analysis' function in WinRHIZO. This subsampling avoided the inclusion of thicker transport roots and allowed us to obtain values that were representative for first order roots. We also dried and weighed the aboveground biomass of each plant, and calculated the root weight ratio (i.e. root biomass divided by total biomass).

Experiment on rooting depth

From 15 May to 10 October 2018, we performed an outdoor pot experiment to measure the maximum rooting depth of the species. Up to five seedlings of the species that had germinated (n = 196; Supplementary information) were transplanted individually into 120 cm tall plastic tree shelter tubes (Tubex Standard Plus, <www.tubex.com/products/tree-shelters/tubex-standard-treeshelters/specification.php>), which are normally used in forestry to protect young trees against animals and the elements. We closed the bottoms of these tubes with thick pieces of cotton tissue to be able to use them as pots. The tubes were filled with a mixture of sand and vermiculite (1:1 volume ratio) up to a height of 115 cm. This substrate can be easily penetrated by the roots, and therefore allows each plant to reach its maximum rooting depth quickly. The tree shelter tubes were delivered in packages of five tubes stacked into each other, and they therefore came in five diameter classes (8.0, 8.4, 10.0, 10.8 and 12.0 cm). To avoid that tube diameter would be confounded with species identity, each of the five seedlings per species was planted in a different tube-diameter class. We placed the tubes upright in a randomized design in the Botanical Garden of the University of Konstanz (47°41′24.0″N, 9°10′48.0″E; see Supplementary information for pictures).

We planted 734 plants but, due to early mortality, we had to replace 126 of them within the next three weeks. The growth period therefore ranged from 16 to 19 weeks. The experiment took place during the summer of 2018 (mean temperature: 19.5°C, min/max 2.5/37.4°C; relative humidity: mean 74%, min/max 22.7/100%). All plants were fertilized once a week with 60 ml of a standard nutrient solution, and watered regularly from above. We harvested the plants in October 2018. Each tube was sliced open, and we measured the distance from the top of the substrate to the deepest root.

Traits from databases and data imputation

Data on the aboveground traits specific leaf area (230 species) and height (228 species) were obtained from the LEDA database (Kleyer et al. 2008). Data on bud-bank size (230 species) including stem and root-derived buds occurring belowground or at the soil surface was obtained from Klimešová et al. (2017). In addition, mycorrhizal status was extracted from the FungalRoot database (Soudzilovskaia et al. 2020). We assigned the corresponding genus-level mycorrhizal status for each of our species (241 species) included in the analysis. Though most of our species are considered either obligatorily arbuscular-mycorrhizal (167 species), facultatively arbuscular-mycorrhizal (57 species) or non-mycorrhizal (16 species), *Helianthemum nummularium* is considered ectomycorrhizal. Therefore, it was grouped with the obligatorily arbuscular-mycorrhizal species to form the obligate-mycorrhizal category (168 species).

Although for each of the traits we had data for 196 (rooting depth) to 311 (seed weight) species, the number of species with complete data for all traits was 170. Therefore, we did phylogenetically informed imputation of missing data for the 241 species that germinated and survived until trait measurement in at least one of our two experiments. Data imputation is a powerful but still underutilized tool that increases sample size – and thus statistical power – and reduces potential biases that might occur if the species with missing data are a non-random subset (Nakagawa 2015). Imputation can perform well with up to 50% of missing data (Graham 2009). In our case, 4.6% of the trait values were missing and had to be imputed (see Supplementary information for details on the imputation procedure). We also ran all analyses for the subset of 170 species with complete data (i.e. without imputed data), and the results were largely similar to the analyses of the 241 species with partly imputed data (Supplementary information). Because the analyses with the imputed data allowed us to include more species (i.e. increase statistical power and generality), we present only those results in the main text. The phylogenetic tree of the species used, their standardized trait values and phylogenetic signal can be found in Supplementary information.

Species abundance and occurrence frequency

To quantify each species' commonness from local scale abundance to global naturalization success, we used four different data sources.

The biodiversity exploratories

To obtain information on local abundance and occurrence frequency of our study species in German grasslands, we used data from the Biodiversity Exploratories grassland-composition surveys. In each of the three regions, ca 500 so-called grid plots (GPs) and a subset of those, the 50 so-called experimental plots (EPs), have been monitored for biodiversity measures. The plots are 50 × 50 m, and in each of those there is a subplot of 4 × 4 m, in which the relative abundance of each plant species has been determined. In the 1494 GPs, vegetation was sampled once from 25 May to 15 August 2007. In May 2009, 138 plots were re-assessed and earlier relevés were discarded, because they were considered unreliable as the vegetation had been recorded too late in the season of 2007 (Socher et al. 2013). Of our 241 study species, 213 were present in that census of the GPs (Supplementary information), and, when present in a plot, they covered on average 2.8% of the plot (min: 0.27%; median: 1.45%; max. 17.16%). For the 150 EPs, the vegetation data were collected annually between mid-May and mid-June from 2008 to 2016, and we averaged the data across years. Of our 241 study species, 239 were present in the EPs vegetation survey, and, when present in a plot, they covered on average 1.05% of the plot (min.: 0.01%; median: 0.34%; max.: 13.05%). Two study species, *Spergula arvensis* and *Taraxacum campylodes*, had been excluded because their names were included in an earlier version of the vegetation survey due to misidentification. While there are 10 times more GPs than EPs, the latter include data over a longer period. For both the GPs and EPs, we used two distribution metrics for each species: the occurrence frequency defined as the number of plots in which a species is present divided by the total number of plots, and the local abundance defined as the mean cover of a species across all the plots where it is present. Because it is based on the presence–absence only, the occurrence frequency estimates how frequent a species is within grasslands in Germany. The average abundance, on the other hand, which is calculated using abundance data for only those plots where the species occurs, estimates how dense the populations of the species are on average.

FloraWeb

For information on the occurrence frequency in all of Germany, irrespective of habitat type, we obtained data from the German plant distribution atlas of NetPhyD and BfN through the FloraWeb data portal (Bundesamt für Naturschutz 2013). For each species, we extracted the number of grid cells in which the species has been reported. Each grid cell is about 130 km^2, and there are 2995 grid cells in total. Of our 241 study species, 235 had grid-cell data available (Supplementary information).

Euro+Med PlantBase

To obtain information on the extent of the native distribution in all of Europe and its adjacent Mediterranean regions, we used Euro+Med PlantBase (PESI 2015). This on-line database provides information on the presence of vascular plant taxa in 117 regions (mostly countries) covering all of Europe and the Mediterranean regions of North Africa and the Near East. Of our 241 study species, 237 species were found in Euro+Med PlantBase, and for those we extracted the total number of regions with native occurrences (Supplementary information). The four remaining species, *Cerastium nutans*, *Erigeron canadensis*, *Matricaria discoidea* and *Medicago* × *varia*, are not native to the region.

GloNAF

As 237 of our 241 study species are native to Europe, we also assessed the extent of their global occurrence as naturalized alien species, using the Global Naturalized Alien Flora (GloNAF) database, ver. 1.2 (van Kleunen et al. 2019). GloNAF is a compendium of lists of naturalized alien plant species for 1029 regions covering >80% of the terrestrial ice-free surface. Of our 241 study species, 221 species had at least one record in GloNAF. For those species, we extracted the number of regions in which they are naturalized, and for the 20 species without GloNAF records, we set the number of GloNAF regions equal to zero.

Statistical analyses

All statistical analyses were performed in R ver. 3.6.1 (<www.r-project.org>). To test whether more abundant and more widespread species have particular trait values, we used generalized linear models in which the response variables were the different measures of species commonness and the predictors were a selection of trait mean values. For number of occurrences in GloNAF regions, and in grassland GPs and EPs, we used negative binomial error distributions (with a log-link function). As the number of occurrences in FloraWeb grid cells and Euro+Med regions did not follow negative binomial or Poisson error distributions, we instead analysed the proportion of FloraWeb grid cells and Euro+Med regions in which a species had been recorded, with a binomial error distribution. To account for overdispersion, we used the 'quasibinomial' setting. For analyses of the mean local abundance (i.e. the cover proportion) of the species in the GPs and EPs, we used a gamma conditional distribution (with log-link function).

For each commonness measure, we used a multivariate model with ten traits as predictors. We a priori chose traits that represent different aspects of plant functioning and that had relatively low pairwise correlations (all $r \leq |0.49|$, Supplementary information) to minimize multicolinearity (the maximum generalized variance-inflation factor of a model was 3.32). We used the following traits: individual seed weight (measured on seeds ordered for the experiments), specific root length, root tissue density and fine roots diameter (measured in the root-system morphology experiment), maximum rooting depth (measured in the rooting-depth experiment) and bud-bank size, height, specific leaf area and mycorrhizal status (from trait databases). Seed weight was log transformed. To facilitate interpretation of and comparison between model coefficients, each trait was scaled to a mean of zero and a standard deviation of one (Schielzeth 2010). To test for potential non-linear effects of traits, orthogonal polynomial terms of second degree (i.e. quadratic terms) were also included for each trait, using the *poly* function. To estimate the proportion of variance explained by the models, we calculated delta R^2 values, applicable to all distributions and link functions, according to Nakagawa et al. (2017) using the package MuMIn (Barton and Barton 2015). To assess whether belowground traits explained more variance in commonness measures than aboveground traits, we also extracted delta R^2 values for models using only the three aboveground predictors and for models using only the three belowground predictors with the highest standardized coefficients. To account for phylogenetic non-independence of the study species, the models were also run using phylogenetic relatedness of species as a variance–covariance matrix (for details, see Supplementary information). Although the significances of the trait effects differed in some instances between the non-phylogenetic models and the phylogenetic ones, the directions of the effects were largely the same in both types of models (compare Fig. 1 and Supplementary information). Therefore, we only present the results of the non-phylogenetic analyses in the main text.

Results

All of our species commonness metrics were significantly related to at least three of the ten traits considered, including both above- and belowground traits (Fig. 1). The abundance measures in the grassland EPs and the occurrence in the EPs and GPs were associated with the largest number of traits (Fig. 1). The delta R^2 values ranged from 0.02 for the model on occurrence frequency in the native range (i.e. the proportion of occurrences in Euro+Med) to 0.42 for the model on abundance in the EPs (i.e. the mean cover of a species when present in a grassland plot; Fig. 1, Table 1). When we reduced the models to either include only the three aboveground traits or the three best belowground traits, the variation explained by the belowground-trait models was equal or greater than the variation explained by the aboveground-trait models for all species commonness metrics, except frequency of occurrence in Germany and in the grassland EPs (Table 1).

Root-tissue density was a significant predictor in all models (Fig. 1). Species with low root-tissue densities were consistently more common than species with high root-tissue densities across all spatial scales considered (i.e. all linear coefficients were negative and significant; Fig. 1). For occurrence frequency outside the native range, the coefficient of the quadratic term was also significantly negative (Fig. 1), indicating that this commonness metric was highest for species with intermediate root-tissue densities (Fig. 1, Supplementary information).

Specific leaf area (SLA) was positively associated with species commonness in most large spatial scale models (Fig. 1). Occurrence frequencies outside their native range, in Germany, and in the grassland GPs and EPs increased with SLA, and sometimes slightly decreased again at higher SLA values. However, SLA had no significant effect on the abundance within GPs and EPs (Fig. 1, Supplementary information).

Bud-bank size was also a significant predictor in most models, but its effects on species commonness varied with spatial scale (Fig. 1). At large spatial scales, occurrence frequencies were highest for species with either small or large bud-bank sizes and lowest for species with intermediate ones

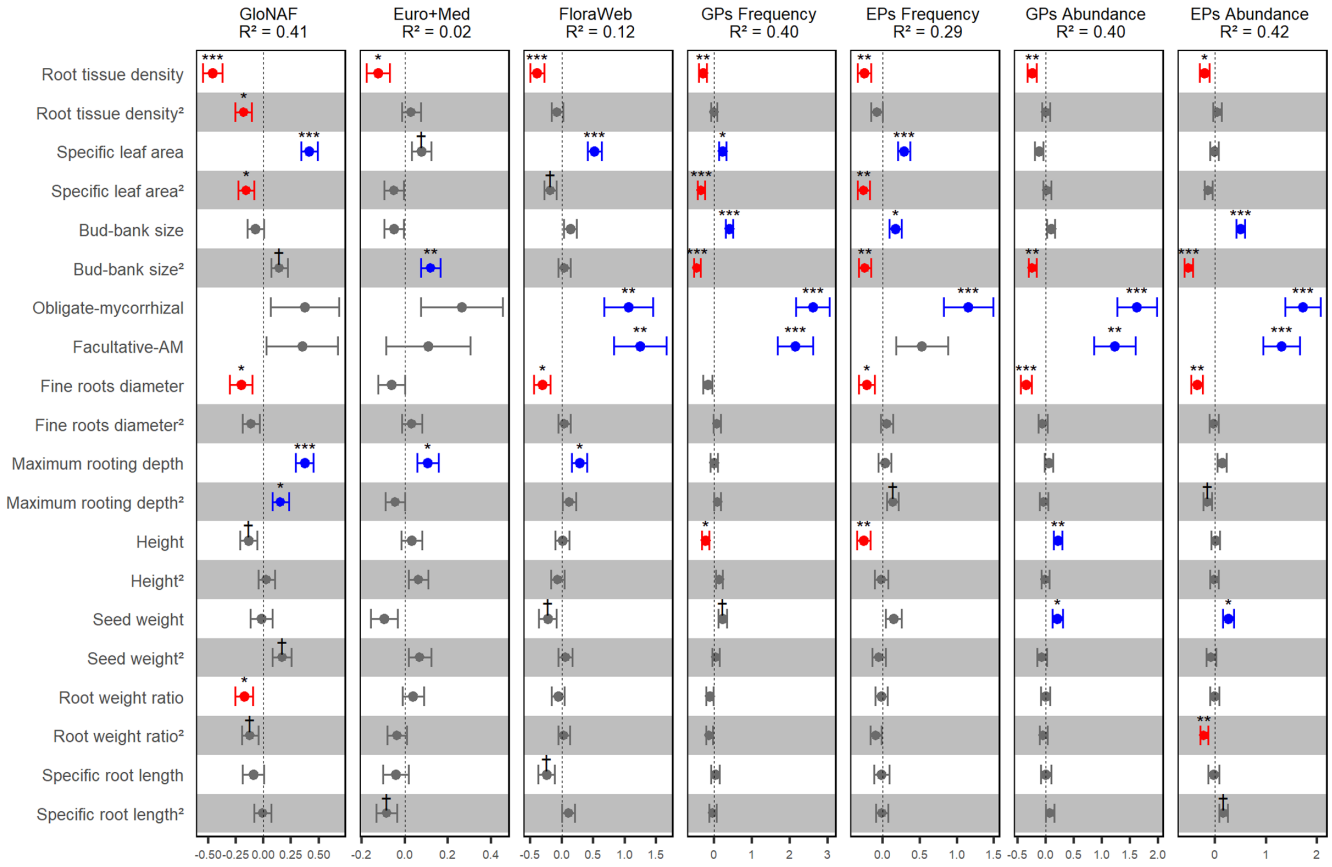

Figure 1. Estimates of trait effects on different commonness metrics of German grassland species from generalized linear models. On the y-axis are the 10 traits used as predictors, with a linear term (white rows) and a quadratic (non-linear) term (grey rows) for each trait. The errors bars around the estimates are standard errors. Significant negative and positive estimates are marked in red and blue, respectively. In addition, estimates with $p < 0.001$ are indicated with ***, estimates with $p < 0.01$ with ** and estimates with $p < 0.05$ with *. Marginally significant estimates ($p < 0.1$) are indicated with †. The spatial scale of the commonness metric decreases from left to right. GloNAF: number of regions in which a species is naturalized (number of species, n = 241); Euro+Med: number of regions in Europe and the Mediterranean basin in which a species is native (n = 237); FloraWeb: number of grid cells in Germany in which a species is present (n = 235); GPs Frequency: number of grassland grid plots in which a species is present (n = 213); EPs Frequency: number of grassland experimental plots in which a species is present (n = 239); GPs Abundance: mean species cover in grassland grid plots in which the species is present (n = 213); EPs Abundance: mean species cover in grassland experimental plots in which a species is present (n = 239). Delta R^2 was calculated according to Nakagawa et al. (2017).

(marginally and significantly positive coefficients of the quadratic terms for the numbers of GloNAF and Euro+Med regions, respectively; Fig. 1, Supplementary information). On the other hand, occurrence frequencies and abundances in the grassland GPs and EPs increased linearly or asymptotically with bud-bank size (Fig. 1, Supplementary information).

Obligate-mycorrhizal and facultative-mycorrhizal species were consistently more frequent and more abundant than non-mycorrhizal species, although not always significantly so for occurrence frequencies at larger spatial scales (Fig. 1, Supplementary information).

Fine root diameter had a negative effect on the occurrence frequencies outside the native range, in Germany, in the EPs and on abundance in the GPs and EPs (Fig. 1, Supplementary information).

The other traits were only significant predictors in a few of the models of species commonness (Fig. 1). Maximum rooting depth was non-linearly positively associated with occurrence frequency outside the native range, and was positively associated with occurrence frequencies in the native range and Germany, but not significantly in the EPs and GPs (Fig. 1, Supplementary information). Plant height was not significantly associated with commonness at the larger spatial scales, but was negatively associated with occurrence frequency in the GPs and EPs and positively with abundance in the GPs (Fig. 1, Supplementary information). Seed weight tended to have negative but non-significant associations with commonness at the larger spatial scales, but positive significant associations with abundances in the GPs and EPs (Fig. 1, Supplementary information). Root–weight ratio was negatively associated with occurrence frequency outside the native range, with an optimum in the mid-lower range of the trait, which was also the case for abundance in EPs (Fig. 1, Supplementary information). Specific root length

Table 1. Delta R^2 of models explaining species commonness using a different set of predictors. On the two first lines are the R^2 values for models with the three predictors with highest explanatory power aboveground and belowground. On the last line are the R^2 values for models with all 10 traits used as predictors.

	GloNAF	Euro+Med	FloraWeb	GPs Frequency	EPs Frequency	GPs Abundance	EPs Abundance
Specific leaf area, seed size, height	0.18	0.01	0.06	0.16	0.16	0.15	0.16
Root tissue density, bud-bank size, mycorrhizal status	0.24	0.01	0.04	0.31	0.13	0.28	0.35
All the predictors (10 traits)	0.41	0.02	0.12	0.40	0.29	0.40	0.42

was not significantly associated with any measure of commonness (Fig. 1). However, it tended to be negatively associated with occurrence frequency in Germany and the highest native occurrence frequency was associated with intermediate values (marginally significant effects in Fig. 1, Supplementary information).

Discussion

We tested how above- and belowground functional traits of grassland species related to their commonness across multiple spatial scales. Among the 241 study species, low root-tissue density was identified as important for all commonness metrics. However, the effects of the other traits were frequently dependent on the commonness metric considered. They notably differed between the occurrence frequency metrics, capturing how widespread a species is, and the abundance metrics, capturing the mean density of individuals of a species where they occur. For example, while specific leaf area was positively and asymptotically related to the large-scale commonness metrics, it was not related to the local abundance in German grasslands. This illustrates that some traits may have different effects on different dimensions of species rarity and commonness. Moreover, we found that many of the effects had significant non-linear effects, in most cases with the highest commonness-metric value at intermediate trait values. While all previous studies on the importance of functional traits for commonness focussed on aboveground traits that are easy to measure or available in databases (Cadotte and Lovett-Doust 2002, Cornwell and Ackerly 2010, Gabrielová et al. 2013, Arellano et al. 2015), our study shows that belowground traits can also explain a significant amount of variation in species commonness.

The spatial scale of commonness ranged from local abundance in 16-m^2 grassland plots in Germany (GPs and EPs) to the global occurrence outside the native range (number of GloNAF regions). While the local scale abundance data are restricted to a single habitat type, the occurrence at larger spatial scales also covers other habitat types (e.g. 86% of the area in Germany is not used as grassland; DESTATIS 2019). Each habitat type might select for different values of a trait (Lososová et al. 2006, Shipley et al. 2017), and species that can occur in many different habitat types (i.e. are habitat generalists) may differ in their trait values from those of habitat specialists. Future studies should therefore try to separate the effects of functional traits on range size from those on habitat generalism.

We found varying degrees of consistency in the trait values of common species across spatial scales. Root-tissue density was the only trait with a consistent effect on all commonness metrics. Probably, a low root-tissue density, which is indicative of a high resource-acquisition-rate strategy (Kramer-Walter et al. 2016) is beneficial in nutrient-rich habitats, which have locally and globally become more widespread as a consequences of agriculture and atmospheric nitrogen deposition. On the other hand, the effect of specific leaf area, an aboveground trait associated with the resource-acquisition strategy (Lambers and Poorter 1992, Onoda and Wright 2018) depended on the spatial scale of the commonness metric. Occurrence frequencies at all spatial scales tended to asymptotically increase with specific leaf area, which is in line with the frequent observation that high specific leaf area promotes invasion success (Pyšek and Richardson 2008, van Kleunen et al. 2010). However, abundance in the grassland plots was not related to specific leaf area, possibly reflecting that persistence under highly competitive pressures in dense grasslands could require a more conservative growth strategy.

Bud-bank size had an effect on most commonness metrics, but the direction and shape of the relationship varied a lot. Species with intermediate or large bud-banks had the highest abundance and occurrence frequency in the grassland plots. A large bud-bank is essential for regrowth of long-lived perennials after e.g. grazing or mowing (Ott et al. 2019). On the other hand, species with small bud-banks, as well as those with large bud banks, tended to have larger naturalized ranges and higher occurrence frequencies in the native range than species with intermediate bud-bank sizes. Although buds themselves are not very costly (Vesk and Westoby 2004), they require bud-bearing organs and nutrient reserves, which may tradeoff with seed production (Herben et al. 2012, 2015). Thus, species with small bud banks, which are more likely to be short-lived, may invest more in seed production, resulting in a higher dispersal ability and larger native and naturalized distributions.

The obligate or facultative interaction with mycorrhizal fungi, mostly arbuscular mycorrhiza, had a positive effect on commonness metrics in the grassland plots and occurrence frequency in Germany. Mycorrhizal plants also tended to be more widely naturalized around the globe, confirming the

results of a recent global analysis (Pyšek et al. 2019), although this effect was not statistically significant. In return for carbon, mycorrhizal fungi provide plants with nutrients and improve their resistance against various stresses. These benefits of the interaction for plants could allow them to survive and reproduce in a greater variety of habitats and environmental conditions than non-mycorrhizal species. Mycorrhizal plants are found in a large variety of habitats (van der Heijden et al. 2015), but could take particular advantage of the minimally disturbed soil in managed grasslands where the mycelium networks can be preserved over several years (Read and Birch 1988). On the other hand, Brassicaceae, which are predominant in our non-mycorrhizal species set (Supplementary information), are more characteristic of disturbed habitats, typical for where these species frequently grow outside their native range. As a consequence of the strong phylogenetic signal in mycorrhizal status (Supplementary information) and the small number of non-mycorrhizal plants in our dataset (16), none of the mycorrhizal effects on commonness remained significant after accounting for phylogenetic non-independence of the species (Supplementary information). The results on the effects of mycorrhizal status on commonness should thus be interpreted with caution.

Thin roots generally characterized common species in our study at both large and small spatial scales. Furthermore, root-tissue density was lower in common species, indicating the tendency to develop 'cheap' root systems, in terms of carbon. Thin, but especially low-density roots potentially have shorter lifespans than thick roots or roots with dense tissues (Ryser 1996, Ma et al. 2018), though the functional mechanisms underlying these relationships differ between these two traits (Weemstra et al. 2016, Bergmann et al. 2020). They could potentially exploit more soil volume per unit of carbon invested. This could be an advantage in both grasslands and anthropogenic habitats, which are generally fertile, and thus could explain why thin roots are more common among both highly naturalized species and dominant species in German grasslands. The specific costs and benefits of root diameter and root tissue density in different environments are however still poorly known (Laliberté 2017).

Maximum rooting depth was positively related to commonness metrics at the largest spatial scales. Deep roots allow a plant to take up water with nutrients from deeper soil layers, increasing survival and growth, particularly when the surface soil regularly dries out (Comas et al. 2013). As most of the agriculturally used grasslands in Germany are mesic (European Environment Agency 2019), this could explain why rooting depth was not significantly associated with occurrence frequency and abundance in the grassland plots. At the larger spatial scales, which also cover other habitat types, species with deep roots might be more persistent. For naturalization success, however, there was a significant non-linear effect of rooting depth as both deep-rooting and superficially rooting species were most successful. This could indicate that the alternative strategy of lateral spread to acquire resources and avoid competition with deeper rooting species (Fitter 1986) might also be beneficial at the global scale.

Height of the plants was not significantly related to commonness of the species at the largest spatial scales. However, it tended to be positively (marginally significantly) associated with naturalization success, which corroborates numerous studies on naturalization and invasion success that found that tall species were more successful (Pyšek and Richardson 2008, Bucharova and van Kleunen 2009). Interestingly, while plant height increased abundance in the German grassland plots (at least in the GPs), it decreased the occurrence frequency in those grasslands. On the one hand, tall plants, when they occur somewhere, might be competitively superior and become dominant, whereas, on the other hand, small plants might be less at risk of losing reproductive organs due to mowing or grazing.

The effect of seed weight on species commonness metrics was positive at the plot scale and tended to be negative or absent at larger spatial scales. The finding that species with heavy seeds tended to be more frequent and abundant in the grassland plots, most likely reflects that large amounts of resources stored in seeds increase seedling survival under the strong competition in grasslands (Moles and Westoby 2004, Kempel et al. 2013). Species with light seeds, on the other hand, might have a higher reproductive output (Moles and Westoby 2006), could potentially disperse over longer distances (Tackenberg et al. 2003, Thomson et al. 2011) and could persist longer in the seed bank (Garnier and Navas 2012). At the larger spatial scales, this benefit of small seeds could have compensated or overcompensated the reduced seedling survival chances.

We found that species that are abundant in grasslands are typically characterized by thin, mycorrhizal, low-density roots, which promote the uptake of belowground resources. In grasslands, belowground organs are of particular importance, as net primary production allocated belowground could be more than 80% (Lauenroth and Gill 2003). Rhizomes, lignotubers and belowground stems can allow plants to resprout and survive disturbances, such as mowing and grazing, and promote regrowth after unfavourable seasons. The importance of bud-bank size in grasslands emphasizes the need to integrate these different belowground organs in the study of functional traits linked to species dominance (Ottaviani et al. 2020). The patterns for commonness metrics at larger spatial scales, at least those in the native ranges, were less clear. Indeed, plant traits explained large proportions of the variation in local abundance and occurrence frequency in the grasslands (>25%; Table 1), whereas the proportion of variation in occurrence frequency in the native range and in Germany was very low (2% and 12%, respectively; Table 1). This suggests that plant traits could be good predictors of species commonness if one considers a single habitat type, but that this is less the case for commonness metrics at large spatial scales that are not habitat specific. However, a notable exception is the global naturalization success of the species, as 41% of the variation in occurrence frequency outside the native range was explained by the plant functional traits. Possibly, this reflects that most naturalizations happen in anthropogenic environments (Chytrý et al. 2009), and thus largely in a single habitat type.

The plant economics spectrum postulates that the high specific leaf area typical for 'acquisitive' plants should be mirrored belowground by a high specific root length, low root-tissue density and a low root diameter (Prieto et al. 2015). Indeed, specific leaf area was negatively correlated with root-tissue density, but it was not significantly correlated with specific root length and diameter of the fine roots (Supplementary information). Although the traits were not strongly correlated at the species level, species common at the larger scales were more likely to have a high specific leaf area, a low root tissue density and thin roots. This decoupling from the plant economic spectrum at the species level has previously been found for grassland plants (Bergmann et al. 2017) as well as tree seedlings (Kramer-Walter et al. 2016) and supports recent findings emphasizing that specific root length and diameter vary independently from the fast to slow economics spectrum (Bergmann et al. 2020). Seed weight and plant height, the other aboveground traits frequently used in studies on functional ecology of plants, were also not strongly correlated with the belowground traits in our study. We measured the diameter of fine roots, which has been proposed to be a proxy of multiple physiological and anatomical traits related to the resource-acquisition strategy (Guo et al. 2008, Wen et al. 2019) and notably of mycorrhizal colonization (Ma et al. 2018, Bergmann et al. 2020). Abundant species in grasslands were characterized with having thin roots but also an obligate mycorrhizal status, suggesting that direct measurements of mycorrhizal colonization and physiological traits would improve our understanding of the links between traits and functions (Laliberté 2017). These belowground traits explained a considerable proportion of variation in the commonness metrics, in addition to the variation explained by the three aboveground traits (Table 1). Indeed, for all commonness metrics, except occurrence frequency in the EPs, the belowground traits explained at least as much of the variation in commonness metrics as the three aboveground traits did. Therefore, our results show that aboveground traits cannot always substitute for belowground traits in studies on plant functional ecology.

Conclusions

We here showed that functional traits of common grassland species differed from those of less common ones, but that the pattern depended on the spatial scale of the commonness metric it applies to. Low root-tissue density was the only trait that characterized common species at every spatial scale, from being abundant in German grassland plots to being widely naturalized around the world. We showed that belowground traits are at least as important as the aboveground traits in explaining species commonness at the different spatial scales. The variation in importance and the sometimes-opposing directions of the effects of traits on species commonness at different spatial scales can explain why trait variation is maintained. Our study shows that, for central European grassland species, variation in commonness is related not only to aboveground traits, but also to belowground traits. Therefore, belowground traits should be more frequently considered in studies on plant functional ecology.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j3tx95xbv> (Lachais et al. 2020).

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Author contributions – TL performed the experiments, ran the analyses and wrote the paper. JB collected data and participated in the experiments. MCR contributed to the design of the experiments. MvK designed the experiments, advised on data analysis and extensively revised the paper. All authors contributed substantially to revisions.
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